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EDAPHOSAURUS (REPTILIA, PELYCOSAURIA) FROM THE LOWER PERMIAN OF NORTHEASTERN UNITED STATES, WITH DESCRIPTION OF A NEW SPECIES

David S Berman
Associate Curator, Section of Vertebrate Fossils

Abstract

A new species, *Edaphosaurus colohistion,* is based on the greater portion of a large, presacral vertebral column from the upper part of the Pittsburgh Formation, Monongahela Group, of northwestern West Virginia. *E. colohistion* and fragmentary *Edaphosaurus* specimens from the later Lower Permian Washington and Greene Formations, Dunkard Group, of the Tri-state area constitute a morphological series in chronological order that in some instances conforms and in others deviates from the well-documented evolutionary trends seen in the series of four essentially consecutively occurring Lower Permian *Edaphosaurus* species of the Southwest. On the basis of 1) the evolutionary trends exhibited by the Tri-state edaphosaur series that conform to those of the Southwest series, 2) the large size of *E. colohistion,* and 3) the numerous, typically Lower Permian amphibians previously reported from the same locality as *E. colohistion* and from various levels in the lower half of the Dunkard Group, it is suggested that the Pittsburgh Formation, or at least its upper levels, and the Dunkard Group are correlative with the Lower Permian Wichita and lower Clear Fork Groups of north-central Texas and that the Wolfcampian-Leonardian Series boundary lies near the base of the Greene Formation. Geographic isolation of the Dunkard basin from the Micontinental basin complex is offered as an explanation for the deviations of the Tri-state *Edaphosaurus* series from the evolutionary trends exhibited by the Southwest series. The Tri-state series probably represents a single lineage that evolved in place and independently from the southwestern forms.

Introduction

The herbivorous, swamp-dwelling pelycosaur reptile *Edaphosaurus* is widespread both spatially and temporally. Eight species are recog-

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nized from deposits of Late Pennsylvanian and Early Permian age in North America and Europe. The genus is best known, however, from the Lower Permian of north-central Texas, where it is represented by three, consecutively occurring species, *E. boanerges, E. cruciger* and *E. pogonias,* from beds extending from the lower Wichita Group up through the overlying lower Clear Fork Group. They exhibit a progressive increase in overall body size that is accompanied by a decrease in relative sail size, and gradual changes in the vertebral neural spines forming their large dorsal sail. These changes suggest that they represent a species phylum that evolved in place (Romer and Price, 1940). The poorly-known *E. novomexicanus* of New Mexico, the only other Lower Permian *Edaphosaurus* species of North America, is viewed as a morphological antecedent to the Texas series. In the Tri-state area of Pennsylvania, West Virginia, and Ohio, *Edaphosaurus* is known from a number of fragmentary specimens from the Upper Pennsylvanian and Lower Permian. The earliest occurring specimen, a small fragment of neural spine from the middle of the Conemaugh Group, was first described by Case (1908) as *Naosaurus raymondi. Naosaurus* was later synonymized with *Edaphosaurus* (Romer and Price, 1940). In 1952 Romer described all the then known *Edaphosaurus* specimens from the Tri-state area. On the basis of overall body size and neural spine structure he referred those specimens from the Washington and the base of the Greene Formation to *E. boanerges* and those from the middle and upper Greene Formation to *E. cruciger.* Since Romer's (1952) report, additional *Edaphosaurus* specimens have been discovered in the Tri-state area. Most important among these is the greater part of a presacral vertebral column, including the dorsal sail, from the upper Pittsburgh Formation, Monongahela Group. This is the first *Edaphosaurus* specimen reported from the Monongahela Group and, though it has been identified as *E. boanerges* (Lund, 1972, 1975, 1976), it has not been described. It is notable for its large size, which is equal to that of *E. boanerges* from the Lower Permian of Texas. This is a principal reason for believing that the Pittsburgh Formation is Lower Permian and not Upper Pennsylvanian as most authors believe; Pennsylvanian members of this genus are much smaller than their Permian descendants. The combined features of overall size and structure of the neural spines distinguish the Monongahela form as a new species, *E. colohistion*.

Viewed in chronological order the Monongahela-Dunkard edaphosaurs exhibit changes that in some instances parallel and in others deviate from the well-established evolutionary trends of the Lower Permian species of the Southwest. Similarities in evolutionary trends of both groups permit stratigraphic correlations between the Pittsburgh Formation and the overlying Dunkard Group, and the classic Lower

Permian terrestrial section of north-central Texas. Previously described amphibians from the same locality in the Pittsburgh Formation from which came the holotype of *E. colohistion* and from various horizons in the lower half of the Dunkard Group, though broadly reinforcing correlations based on *Edaphosaurus*, necessitate some minor reassessments. Differences in trends between the edaphosaurs of both areas are, however, sufficient to suggest that those from the Tri-state may represent a single lineage that evolved in place and independently from those of the Southwest. This is accounted for by geographic isolation of the Dunkard basin by the end of the Pennsylvanian.

Abbreviations CM and USNM are used to refer to collections of the Carnegie Museum of Natural History and the National Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Order Pelycosauria
Family Edaphosauridae
Genus *Edaphosaurus* Cope 1882
Edaphosaurus colohistion, new species

Holotype.—CM 23513 consists of an articulated, or nearly articulated, series of 14 essentially complete presacral vertebrae believed to include cervicals 6 and 7 and dorsals 8 through 19 (Fig. 1). Disarticulated but closely associated with the partial vertebral column are four or five intercentra, two incomplete vertebrae and numerous neural spine fragments near both ends of the column, and numerous ribs. The holotype was collected by Dr. Richard Lund of Adelphi University in 1969.

Horizon.—Limestone "B" of the Pittsburgh Formation, Monongahela Group. The age of the Pittsburgh Formation has been generally accepted as Late Pennsylvanian, Virgilian, but is considered here, at least its upper levels, as probably Early Permian, Wolfcampian.

Locality.—Road cut on Interstate Highway 70 about ½ mi east of Elm Grove, West Virginia. The deposit from which the holotype was collected has been described by Lund (1972:51) as a meander cutoff channel that filled very slowly.

Diagnosis.—Differs greatly in size from all *Edaphosaurus* species except the Lower Permian *E. boanerges* and *E. novomexicanus*. *E. colohistion* is distinguished from *E. boanerges* in the following features of its neural spines: form a relatively much shorter sail; much closer spacing of lateral tubercles; no anteroposterior expansion of distal portions of posterior cervical or anterior dorsal spines; sail decreases in height at the same rate anteriorly and posteriorly from its highest level.

Fig. 1.—*Edaphosaurus colohistion*, holotype, CM 23513.

E. colohistion is similar to *E. novomexicanus* in lacking any anteroposterior expansion of the neural spines but differs in being somewhat larger, in its greater development of the basal tubercles of the posterior cervical spines and in its greater cross-sectional thickening of the distal portions of the cervical spines.

Etymology.—Greek *kolos,* meaning docked, shortened or stunted, and *histion,* meaning sail, referring to its relatively small sail.

Description.—The holotype (Fig. 1) consists of a series of 14 essentially complete, articulated, or nearly articulated, presacral vertebrae; close to either end of this series are two incomplete vertebrae and numerous spine fragments. Four, or possibly five, disarticulated intercentra and numerous ribs lie near the articulated column. All but a few of the articulated vertebrae are exposed in right lateral view and their centra show considerable lateral crushing; the centra exposed in end view retain their circular outline. The entire specimen, especially the neural spines, exhibits numerous fractures along which there has been in most cases some separation. Most of the spines appear to be complete and by way of comparison with the restoration of *Edaphosaurus boanerges* by Romer and Price (1940:391, Fig. 66) the longest spine of *E. colohistion* probably belongs to the fourteenth vertebra and, therefore, lies near the middle of the presacral series which in *Edaphosaurus* is believed to consist of somewhere between 24 and 27 vertebrae. If this identification is correct, the articulated series would include the posterior two cervicals and the anterior 12 dorsals. Crushing and incomplete preservation makes regional differentiation of the centra impossible; it can be said, however, that the centra exhibit no noticeable differences from those of other members of this genus. Of the centra complete enough or sufficiently exposed to take one or more of the following measurements, the recorded size ranges are: (1) length of centrum, 30.0 to 34.5 mm; (2) width of centrum, 24.0 to 25.0 mm; (3) height of centrum, 24.0 to 29.0 mm. Averages for these measurements for the dorsal vertebrae are given in Table 1. Crushing of the laterally exposed centra has undoubtedly slightly increased their height and decreased their width; undistorted, these two dimensions would probably be nearly equal, about 25 mm. As is typical of *Edaphosaurus,* the intercentra are small, anteroposteriorly narrow, low crescents. According to Romer and Price (1940) the rare occurrence of intercentra in *Edaphosaurus* suggests that most of the intercentra remained cartilaginous.

The structure of the neural spines in *E. colohistion* is in close accord with the pattern in *Edaphosaurus* generally. The proximal portions of the spines are laterally compressed with an anteroposterior length of about 18.0 to 24.0 mm and a transverse width of about 10.0 to 14.0 mm. Just above the first tubercle they taper rather abruptly to a subcircular section, then gradually narrow to their termination. The spine of the presumed fourteenth vertebra, for example, narrows in anteroposterior diameter to 14, 12, and 10 mm at levels of ¼, ½, and ¾ its height. For most of their length the neural spines exhibit a prominent longitudinal ridge on the anterior face, whereas posteriorly there is a longitudinal groove. The longest spine, that of the presumed fourteenth vertebra, is 445 mm long measured from the zygapophyses. The height of the sail appears to decrease by about the same rate anteriorly and posteriorly from its highest point. There is no indication of anteroposterior expansion of the distal portions of the neural spines believed to belong to the posterior cervicals and anterior dorsals such as occurs in varying degrees in Lower Permian species (Romer and Price, 1940).

As is characteristic of *Edaphosaurus* the lateral tubercles or crossbars of the neural spines tend to be arranged in bilaterally symmetrical pairs that occur at rather regular intervals along the spine and form anteroposterior rows with those of successive spines; this pattern, however, becomes increasingly irregular toward the distal ends of the spines

Table 1.—*Measurements (in mm) of vertebrae in* Edaphosaurus; *OLU refers to orthometric linear unit (radius of centrum to the ⅔ power) of Romer and Price (1940). All measurements are of individual elements except those for* E. colohistion *and Southwest species (from Romer and Price, 1940: Table 5) which are averages of dorsal vertebrae.*

Specimen or species	Centrum length	Centrum width	Centrum height	Antero-posterior length of spine at base	OLU value
		Tri-state Edaphosaurs			
CM 8604				18.0	
				17.0	
CM 8540		18.0	17.0		4.16
		17.0	18.0		4.33
				16.0	
				18.0	
CM 23818				16.0	
CM 8601				16.0	
CM 8600				13.0	
USNM 205488		23.0	22.0	17.0	
	28.0	26.0	23.0	19.0	5.53
		25.0	23.0		5.38
	30.0	26.0	26.0	20.0	
	33.0	24.0	25.0	17.0	
Marietta College specimen				19.0	
				18.0	
				17.0	
Edaphosaurus colohistion CM 23513	33.2	24.5	26.1	19.2	5.24
		Southwest Edaphosaurs			
Edaphosaurus pogonias	46.0	36.0	35.0		6.87
Edaphosaurus cruciger	41.0	34.0	34.0		6.61
Edaphosaurus boanerges	34.0	24.0	25.0		5.24
Edaphosaurus novomexicanus	33.0	21.0	21.0		4.79

and the anterior end of the column. Average intertubercular distances for the first seven tubercles of the articulated series of presumed dorsal vertebrae of the holotype are given in Table 3. The lateral tubercles are well developed with rounded ends and become shorter more distally along the spine; as an example, the first six tubercles on the right side of an anterior dorsal spine have lengths of 20, 17, 10, 8, 8, and 5 mm. The tubercles are further reduced distally to nubbins. The highest number of tubercles that I am able to estimate along any one side of a neural spine is about 14.

The ribs of CM 23513 are characteristic of *Edaphosaurus* in being greatly curved throughout their length and in having the tubercula represented by only a slightly raised, rugose area on the shaft.

COMPARISONS

Recognition of *Edaphosaurus* species has been based on vertebral structure, overall size, and to some extent stratigraphic level. On the

Table 2.—*Length of longest neural spines in* Edaphosaurus; *OLU refers to orthometric linear unit of Romer and Price (1940). Measurements for Southwest species from Romer (1948).*

Specimen or species	Longest spine in mm	Longest spine in OLU
Tri-state Edaphosaurs		
USNM 205488	524	96
	420	77
Edaphosaurus colohistion CM 23513	445	85
Southwest Edaphosaurs		
Edaphosaurus pogonias	645	92
Edaphosaurus cruciger	720	109
Edaphosaurus cf. *boanerges*	594	110
Edaphosaurus boanerges	552	108

basis of overall size and neural spine structure *Edaphosaurus colohistion* could be confused with only two of the four species known from the Lower Permian of the Southwest, *E. boanerges* and *E. novomexicanus*.

In overall size, *E. colohistion* falls well within the range of *E. boanerges,* which is best known by a number of excellent specimens from the Wichita Group of north-central Texas (Romer and Price, 1940). Differences in the structure of their vertebral neural spines, however, allow them to be easily separated. The dorsal sail of *E. colohistion* is relatively much shorter than that of *E. boanerges*. As indicated in Table 2, the maximum lengths of dorsal spines published by Romer and Price (1940) for two specimens of *E. boanerges,* representing near minimum and maximum (possibly a separate species) sized individuals, range from over 100 to almost 150 mm longer than that of *E. colohistion*. In terms of the orthometric linear units used by Romer and Price (1940:8) to express linear measurements in values relative to the animal's overall size—one linear unit is defined as equal to the radius of the average sized dorsal centrum to the ⅔ power—the longest spines of the above *E. boanerges* specimens exceed that of *E. colohistion* by 30 units. Whereas in *E. colohistion* the sail decreases in height at the same rate anteriorly and posteriorly from its highest level, in *E. boanerges*, as figured by Romer and Price (1940: Fig. 66), it decreases at a lesser rate posteriorly. As indicated in Table 3 the average distances between the neural spine tubercles are noticeably smaller in *E. colohistion* than in *E. boanerges*. The number of tubercles per spine appears to be about equal in the two species; the highest count of tubercle pairs that Romer and Price (1940) were able to see on a specimen of *E. boanerges* was 16, as compared to 14 for *E. colohistion*. Romer and Price (1940) point out that in *E. boanerges* there is a definite, though slight, anteroposterior expansion of the cervical spine tips; this does not appear in *E. colohistion*.

Table 3.—*Average distances (in mm) between first six tubercles of dorsal neural spines in* Edaphosaurus; *extremes are in parentheses. Measurements for* E. boanerges *from Romer and Price (1940:384).*

Specimen or species	Intervals					
	1–2	2–3	3–4	4–5	5–6	6–7
CM 23818	33	42	49	31	32	
USNM 205488	74 (72–78)	93 (84–105)	57 (48–64)			
Edaphosaurus colohistion CM 23513	34 (28–52)	36 (23–68)	31 (14–45)	30 (15–37)	29 (13–37)	33 (26–38)
Edaphosaurus boanerges	61 (52–70)	55 (37–71)	44 (30–62)	43 (23–58)	40 (27–48)	36 (27–40)

E. novomexicanus, smallest of the North American Lower Permian species of *Edaphosaurus,* is based on a fragmentary anterior half of skeleton from the Abo Formation of northern New Mexico (Romer and Price, 1940). This specimen is somewhat smaller than *E. colohistion*; its orthometric linear unit value is estimated by Romer and Price (1940) to be 4.79, whereas that calculated for *E. colohistion* is 5.24. The type of *E. novomexicanus* includes cervicals 2 through 7 and the centrum and base of the spine of what is believed to be dorsal 12. The cervical spines are nearly complete and show no anteroposterior expansion at their tips; in this feature they are similar to those of *E. colohistion.* Though none of the dorsal spines are preserved, Romer and Price (1940) note that the nature of its cervical spines suggests that the dorsal spines were at least as long as those of later American species; if true, *E. novomexicanus* would differ from *E. colohistion* in having a relatively larger sail. The cervical spines of *E. novomexicanus,* as figured by Williston and Case (1913:77), are considerably more slender than those of *E. colohistion.* The maximum anteroposterior length of the subcircular, distal portions of the posterior cervical spines is about 8 mm in *E. novomexicanus* and about 15 mm in *E. colohistion*; expressed in orthometric linear units, these measurements convert to 1.7 and 2.8 units, respectively. In contrast to *E. colohistion,* the large basal tubercles at the level of the transition from the proximal to the distal portion of the spine of the posterior cervicals are far less developed in *E. novomexicanus.*

EVOLUTIONARY TRENDS IN *EDAPHOSAURUS*

Edaphosaurus *of the Southwest.*—What is known about structural trends in *Edaphosaurus* is based almost entirely on the three consecutively occurring species, *E. boanerges, E. cruciger,* and *E. pogonias,* from the Lower Permian of north-central Texas which probably descended one from another *in situ* and, therefore, constitute a species phylum (Romer and Price, 1940). Romer and Price (1940) estimated their weights at 83, 166, and 186 kg and their lengths at about 250, 272, and 327 cm, respectively. This steady increase in overall size, however, was not accompanied by a similar increase in sail size. As Romer (1948) pointed out and as Table 2 indicates, using greatest spine length as an index to overall sail size, their sails increased only slightly in absolute size, but in terms of orthometric units have ceased to grow and, in fact, the largest member of the series possesses the smallest sail relative to body size.

A number of gradual structural changes in the spines of the three Texas species have been discussed or made obvious in illustrations by Romer and Price (1940: Figs. 66, 67, 68). There is not only a tendency toward greater cross sectional thickening of the spines, but of anteroposterior expansion of the distal portions of the cervical spines. In *E. boanerges* anteroposterior expansion of the cervical spines is slight and extends posteriorly to include the sixth vertebra, in *E. cruciger* expansion is somewhat more prominent and extends to the tenth vertebra, and in *E. pogonias* the spines are greatly expanded to the eleventh vertebra and appear club-shaped in side view. A decrease in number of pairs of lateral tubercles per spine, especially conspicuous at the anterior end of the column, is also exhibited by the Texas species. Concomitantly, there is an increase in the spacing of the tubercles throughout the column; this is most pronounced in the lower portions of the spines and along the entire length of the spines of the anterior half of the column. The three species also exhibit a progressive increase in development of the tubercles. In *E. boanerges* the tubercles become gradually smaller toward the distal end of the spine where they are reduced to nubbins. In the two larger species the tubercles are in general larger, the tips may be somewhat irregularly expanded and those at the distal ends of the spines, particularly in the cervical region, may be closely clustered in groups of two or three, or divide into two or more processes.

In both overall size and morphology of the spines *E. novomexicanus,* a contemporary of *E. boanerges* from New Mexico and Utah (Williston and Case, 1913; Vaughn, 1963, 1966, 1969), is considered by Romer and Price (1940) to be a close antecedent to *E. boanerges*. It is smaller than *E. boanerges,* having an estimated weight of about 63 kg and a length of about 241 cm, and its cervical spines are narrower and show no signs of anteroposterior expansion.

Edaphosaurus *of the Tri-state area.*—In 1952 Romer published a comprehensive report on the vertebrate fossils from the Upper Pennsylvanian and Lower Permian of the Tri-state area; stratigraphic and locality data for these fossils were published by Moran (1952). In Romer's report numerous fragmentary remains, mostly vertebrae, of

Edaphosaurus were referred to either *E. boanerges* or *E. cruciger.* These assignments were based on overall size and neural spine structure. In general he assigned those specimens from the Washington and basal Greene Formations to *E. boanerges* and those from the middle and upper Greene Formation to *E. cruciger.* Reexamination of these specimens and study of new finds, however, indicates that the Tristate *Edaphosaurus* specimens exhibit trends that deviate from some of those of the three consecutive Texas species but conform to others. Only those specimens from the Monongahela and Dunkard Groups having vertebral elements useful in comparing relative overall sizes or in revealing differences in spine structure between individuals are discussed here; *E. raymondi* from the Late Pennsylvanian Conemaugh Group of southwestern Pennsylvanian (Case, 1908) is too incomplete to be useful. The approximate stratigraphic positions of the specimens discussed here are indicated on the generalized geologic column of Fig. 2; in stratigraphic sequence from the lowest occurrence, these specimens include:

CM 23513, *E. colohistion,* holotype (already discussed).

Uncataloged specimen belonging to Marietta College, Ohio, described by Whipple and Case (1930) and consisting of several partial spines preserved in serial order and fragments of spines and ribs from the Upper Marietta Sandstone, Washington Formation, Jackson County, West Virginia (Locality I of Moran, 1952).

USNM 205488, an undescribed specimen consisting of about seven disarticulated but closely associated, well-preserved dorsal vertebrae, some of which are nearly complete, and numerous spine fragments from the Upper Marietta Sandstone, Washington Formation, just south of Belpre, Washington County, Ohio.

CM 8600, proximal portion of spine from Jollytown Sandstone, Greene Formation, Putnam County, West Virginia (Locality 12 of Moran, 1952).

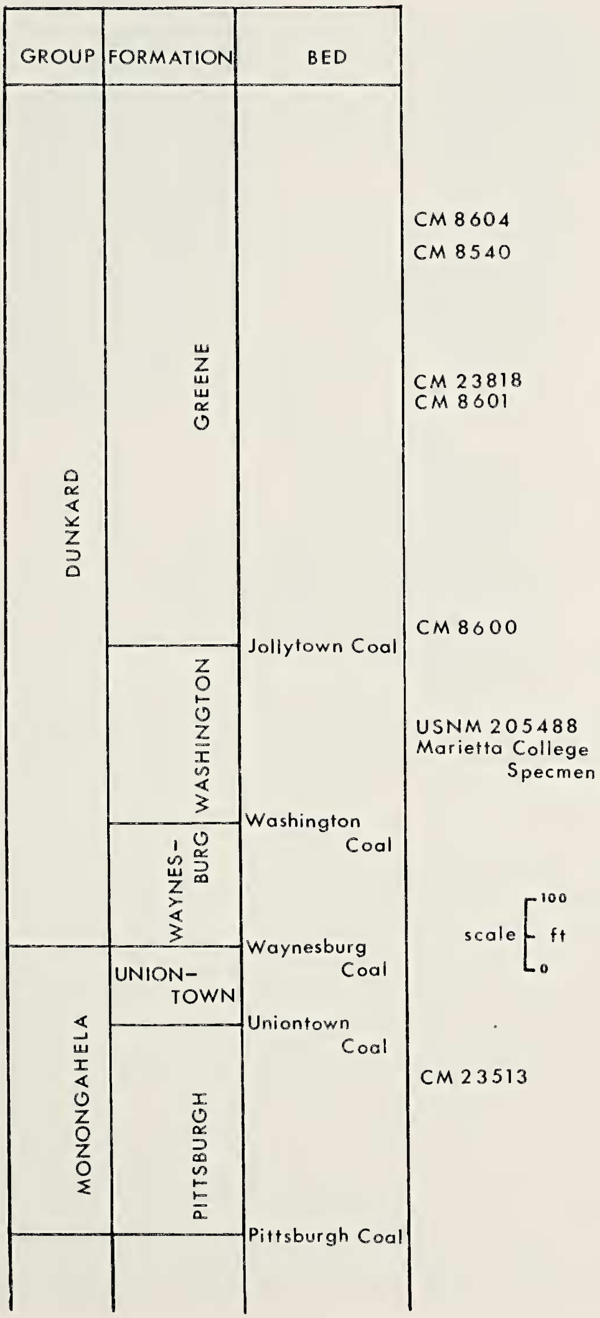
CM 8601, fragments of spine from Middle Rockport Limestone, Greene Formation, Monongalia County, West Virginia (Locality 25 of Moran, 1952).

CM 23818, complete spine from a level between the Middle and Upper Rockport Limestones, Greene Formation, Monongalia County, West Virginia (Locality 28 of Moran, 1952).

CM 8540, numerous fragments of vertebrae and ribs from just be-

→

Fig. 2.—Generalized geologic column of the Upper Pennsylvanian and Lower Permian of southwestern Pennsylvania (after Berryhill and Swanson, 1962) showing approximate stratigraphic positions of *Edaphosaurus* specimens discussed in text.


GROUP
FORMATION
BED
DUNKARD
GREENE
CM 8604
CM 8540
CM 23818
CM 8601
CM 8600
Jollytown Coal
WASHINGTON
USNM 205488
Marietta College
Specmen
Washington
Coal
WAYNES-
BURG
scale
100
ft
0
Waynesburg
Coal
UNION-
TOWN
Uniontown
Coal
MONONGAHELA
PITTSBURGH
CM 23513
Pittsburgh Coal

neath Windy Gap Coal, Greene Formation, Wetzel County, West Virginia (Locality 35 of Moran, 1952).

CM 8604, fragments of spine either from just above limestone that lies 50 ft beneath Windy Gap Coal or from just above the Windy Gap Limestone, Wetzel County, West Virginia (Locality 37 of Moran, 1952).

It is of course realized that there are regional size differences in the presacral vertebrae of *Edaphosaurus* and the use of isolated vertebrae to compare sizes of individuals introduces the chance of some error. Further, among the fragmentary specimens listed above some are obviously not representative of the maximum sizes reached by *Edaphosaurus* at the horizons from which they were collected. It is assumed, however, that the number of specimens considered is large enough to reduce the effects of these errors to a level that will eliminate erroneous conclusions.

Although the Tri-state specimens occur over a wide stratigraphic sequence that undoubtedly represents a considerable length of time, they do not exhibit the marked increase in overall size with time seen in the Texas species and remain within the size range of the earliest occurring Texas species, *E. boanerges* (Table 1). On the basis of centrum size and anteroposterior length of the spine base, USNM 205488 from the Washington Formation shows only a small increase in size over *E. colohistion* from the Pittsburgh Formation. The same measurements for the other specimens from the Washington and Greene Formations indicate individuals of a slightly to moderately smaller size than USNM 205488 and *E. colohistion* CM 23513.

Although the Tri-state edaphosaurs do not appear to increase in overall size with time, their sails may have increased slightly in relative size. The evidence for this is limited to a comparison between *E. colohistion* CM 23513 and USNM 205488 (Table 2). Spine length is available in only two of the vertebrae of USNM 205488; in one the spine is complete and is 420 mm long, whereas in the other the distal half of the spine is missing a small central portion and what is believed to be the end of the spine is represented by impression. If the extent of the latter spine has been correctly determined, its length is 525 mm; expressed in orthometric linear units it is 11 units longer than the longest spine of CM 23513.

Edaphosaurus specimens of the Tri-state area appear to exhibit structural changes in the neural spines that parallel those seen in the southwestern species. Although there is no obvious indication of a tendency toward greater cross sectional thickening of the spines, there is definite evidence of a trend in anteroposterior expansion of the spine tips and greater development of the tubercles of the spines. None of

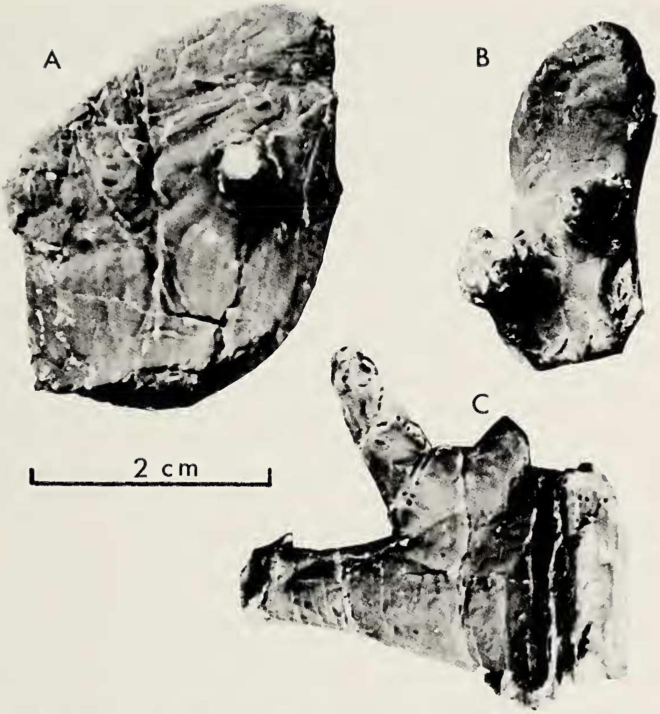


Fig. 3.—A, and B, neural spine tips and C, a small section of neural spine presumably from the cervical or anterior dorsal region of *Edaphosaurus* CM 8540, Greene Formation, Dunkard Group.

the spines of *E. colohistion* CM 23513, including those of the presumed posterior cervicals, show expansion or unusual development of the tubercles. The earliest occurring Tri-state specimen exhibiting expansion of the spine tips is the Marietta College specimen from the Washington Formation. A series of spine tips of this specimen, presumably from the cervical region, are somewhat expanded but the tubercles remain as small nubbins. In these features the Marietta College specimen is similar to *E. boanerges*. CM 8540 is the only specimen from the Greene Formation in which the spine tips from presumably the cervical or anterior dorsal region are preserved (Fig. 3); they exhibit a much greater development compared to those of the Marietta College specimen. One of the spine tips is greatly expanded but its tubercles remain small, two others are only slightly expanded but possess closely grouped, well-developed tubercles; a portion of a fourth spine bears a tubercle with a greatly expanded base from which project two well-developed processes. As pointed out by Romer (1952) these characters suggest a stage of development paralleling that of *E. cruciger* of the Texas edaphosaur series.

There is also limited evidence of a progressive increase in tubercular spacing and a reduction in the number of tubercles per spine in the Tri-state series of edaphosaurs. As Table 3 shows, the spacing of the tubercles in *E. colohistion* is considerably less than in *E. boanerges*. USNM 205488 from the Washington Formation exhibits a very substantial increase in tubercular spacing compared to that in *E. colohistion* and a moderate increase compared to that in *E. boanerges*. A few intertubercular distances are available for the lower portions of four spines preserved in serial order in the Marietta College specimen from the Washington Formation; the measurements are consistent with those for USNM 205488. It is also estimated that the spines of USNM 205488 probably possessed at most about eight pairs of tubercles, a number that is less than the minimums for the dorsal spines of *E. colohistion* and *E. boanerges* (see Romer and Price, 1940: Fig. 66), but is in line with minimum counts for the anterior dorsals of *E. cruciger* or the middorsals of *E. pogonias* (see Romer and Price, 1940: Figs. 67, 68). A complete, isolated spine from the Greene Formation, CM 23818, deviates somewhat from the trends discussed above, but this is probably due to its being from an immature individual. The spine is only 380 mm long with an anteroposterior length at its base of 13 mm. It possesses six pairs of weakly developed tubercles that become smaller distally until they are no longer detectable on the distal third of the spine. The intertubercular spaces are comparable to those in *E. colohistion*.

Discussion

Although most authors consider the Dunkard Group to be Lower Permian, there persists some widely differing opinions concerning its biostratigraphic placement. Using vertebrate, invertebrate, and plant fossils (Barlow, 1975), some consider the entire Dunkard to be Pennsylvanian, others place the Pennsylvanian-Permian boundary at various levels in the Dunkard, some accept the traditional placement of the base of the Permian at or very near the base of the Dunkard, whereas others include all or portions of the underlying Monongahela Group in the Permian. Views based on vertebrates, however, have been fairly consistent and workers have assigned either the Dunkard Group alone (Romer, 1952; Berman and Berman, 1975; Olson, 1975) or with the upper part of the Monongahela Group (Lund, 1975, 1976) to the Lower Permian. In this paper the latter view is supported.

Information presented here indicates that the edaphosaurs from the upper Pittsburgh Formation, Monongahela Group, and the Dunkard

Group do not exhibit a progressive increase in size as in the southwestern species but remain, for the most part, within the size range of *E. boanerges,* smallest member of the Lower Permian *Edaphosaurus* series of Texas. The few exceptions are from the middle and upper Greene Formation and they, in contrast, appear to have an overall size that is smaller than that of *E. boanerges.* The fact that *E. colohistion* attained a size well within the range of *E. boanerges* is interpreted as evidence that the upper Pittsburgh Formation is correlative with the lower Wichita Group. It should also be remembered that *E. colohistion* is larger than *E. novomexicanus*, which occurs in beds in New Mexico and Utah (Williston and Case, 1913; Vaughn, 1963, 1966, 1969) that are considered equivalent to the lower parts of the Wichita Group (Langston, 1953; Romer, 1960). Trends in the anteroposterior lengthening of the upper portions of the anterior neural spines and the greater development of the spine tubercles in the Southwest species appear to have been paralleled in the Monongahela-Dunkard edaphosaurs. These parallelisms suggest that the upper Pittsburgh Formation is correlative with the lower Wichita, the Washington Formation up through the lower and middle Greene Formation with the middle Wichita, and the upper Greene Formation with the upper Wichita Group. These correlations in turn place the Pennsylvanian-Permian boundary at about the middle or lower Pittsburgh Formation and the Wolfcampian-Leonardian Series boundary of the Lower Permian at about middle Greene Formation. Amphibians recently discovered in the Dunkard corroborate in great part the correlations based on *Edaphosaurus,* except that some suggest an equivalence of the Greene Formation and possibly the upper Washington Formation with the Clear Fork Group of Texas. Heading this list is *Trematops* described by Olson (1970) from the Creston Shale just below the Upper Marietta Sandstone, a horizon equivalent to the Washington Coal "A" of the upper Washington Formation. The family to which it belongs, Trematopsidae, is restricted to the Lower Permian and in Texas the three recognized species of *Trematops* are confined to the Clear Fork Group. *Broiliellus* was reported (Berman and Berman, 1975) from the Mount Morris Limestone, Washington Formation (Waynesburg Formation of the nomenclature used in Fig. 2), which is only about 60 ft above the Waynesburg Coal, the top of the Monongahela Group. *Broiliellus,* a well represented and moderately advanced member of the Dissorophidae, includes four species from the Lower Permian of Texas that have a stratigraphic range from the Putnam, lower Wichita Group, to the Arroyo Formation, lower Clear Fork Group. From the same site in the upper Pittsburgh Formation that yielded the holotype of *E. colohistion,* Lund (1972, 1975, 1976) has also collected and identified, or tentatively identified, the amphibians *Diploceraspis burkei* (CM

25206), *Lysorophus dunkardensis* (CM 25653), *Edops* (not cataloged), and *Zatrachys serratus* (CM 25659); the specimen described here as the holotype of *E. colohistion* was identified from this site by Lund as *E. boanerges.* Noting that *D. burkei* is the most common vertebrate from the Greene Formation, that *Zatrachys* is confined to Wichita and Clear Fork equivalents of the Southwest, and that *E. boanerges* is known from the Washington and Greene Formations as well as the Wichita Group of Texas, Lund ascribed a Wolfcampian age to the upper Pittsburgh Formation and suggested that the upper Greene Formation may be equivalent to the basal Leonardian Clear Fork beds of Texas. Considering the vertebrate evidence as a whole, the Pittsburgh Formation, or at least its upper levels, and the Dunkard Group are probably equivalent to the Wichita and lower Clear Fork Groups of Texas with the Wolfcampian-Leonardian boundary lying near the base of Greene Formation.

The observations that the Tri-state edaphosaurs, in contrast to those of the Southwest, do not show a progressive increase in overall size but remain the same size, or even possibly become smaller, and that their sails may have increased, rather than decreased, in relative size may indicate that they evolved in isolation. There are other members of the Dunkard fauna that appear to have developed in isolation from the Lower Permian faunas of the Southwest. I (Berman, 1978) have recently described a new species of the rare, Early Permian pelycosaur genus *Ctenospondylus, C. ninevehensis,* from a very high level in the Greene Formation, the Nineveh Limestone. Though *C. ninevehensis* existed at the same time or very probably somewhat later than the only other member of this genus, *C. casei* from the Lower Permian of Texas (Romer and Price, 1940) and Utah (Vaughn, 1964), the former exhibits a greater primitiveness in a number of features that makes it an ideal predecessor to *C. casei.* Parallel evolution following long-term separation has long been accepted (Beerbower, 1963) as the explanation for the remarkable similarity between the amphibians *Diploceraspis* from the Upper Pennsylvanian and the Lower Permian of the Tri-state area and *Diplocaulus* from the Lower Permian of the Southwest, both noted for their bizarre long-horned skulls.

I (Berman, 1978) have attempted to explain on paleogeographic grounds the possible presence of relictual or endemic forms in the Dunkard fauna. During the Early and Middle Pennsylvanian a shallow, northeastern arm of the Midcontinental basin complex, the Appalachian basin, extended into the Tri-state area. During this time an unbroken habitat zone, or zones, probably allowed free faunal movements between the Tri-state and Midcontinental regions. With the close of the Pennsylvanian, however, expansion of areas of low relief eliminated all of the Appalachian basin except its northeastern termination, which persisted into the Permian as the Dunkard basin. The Dunkard basin was a restricted basin that was bordered on the east and southeast by the active old Appalachian highlands and on the west by the stable continental interior, specifically the Cincinnati Arch. Separated by at least 1,000 mi, it is possible to envision the Lower Permian deltaic faunas of the Midcontinental basin complex and the Dunkard basin as having had different evolutionary histories. With regard to the Monongahela-Dunkard *Edaphosaurus* series, it seems very probable that it represents a single lineage that evolved *in situ* and independently from the Lower Permian species of the Southwest. If this view is accepted, then it seems equally probable that the Dunkard edaphosaurs include two as yet undescribed species—the Washington and lower Greene edaphosaurs pertain to one species and those from the middle and upper Greene to a second. Though this is likely, recognition of new Dunkard *Edaphosaurus* species is best delayed until they can be based on more complete materials.

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